Antagonistic coevolution between multiple quantitative traits: matching dynamics can arise from difference interactions

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ABSTRACT

Coevolution is one of the major drivers of complex dynamics in population ecology. Historically, antagonistic coevolution in victim-exploiter systems has been a topic of special interest, and involves traits with various genetic architectures (e.g., the number of genes involved) and effects on interactions. For example, exploiters may need to have traits that "match" those of victims for successful exploitation (i.e., a matching interaction), or traits that exceed those of victims (i.e., a difference interaction). Different models exist which are appropriate for different types of traits, including Mendelian (discrete) and quantitative (continuous) traits. For models with multiple Mendelian traits, recent studies have shown that antagonistic coevolutionary patterns that appear

as matching interactions can arise due to multiple difference interactions. Here we generalize their findings to quantitative traits and show, analogously, that the multidimensional difference interactions sometimes behave qualitatively the same as matching interactions. While previous studies in quantitative genetics have used the dichotomy between matching and difference frameworks to explore coevolutionary dynamics, we suggest that exploring multidimensional trait space is important to examine the generality of results obtained from one-dimensional traits.

Keywords: bidirectional axis of vulnerability, fluctuating selection, gene-for-gene, matching allele, unidirectional axis of vulnerability

INTRODUCTION

Theories developed from specific models are initially only as general as their underlying models, until they are shown to hold in other modeling frameworks. Hence, it is critical to compare results from a variety of modeling frameworks to test their generality. Antagonistic coevolution in victim-exploiter systems (e.g., prey-predator or host-pathogen systems) has been intensively studied theoretically (Abrams 2000, Nuismer 2017). It is thought to be a major driver for the emergence and maintenance of biodiversity (Thompson 2005) and feedbacks between interacting species can create complex ecological (e.g., Cortez and Weitz 2014) and evolutionary (e.g., Dercole et al. 2010) dynamics. Historically, various coevolution models with differing genetic architectures (e.g., the number of genes involved) and interspecific interactions (e.g., a "matching" vs. a "difference" interaction: see below) have been proposed and analyzed (Nuismer 2017). To account for genetic architecture, one approach is to consider coevolution with a few major genes that interact and produce a discrete phenotype (Mendelian trait-based models, or hereafter Mendelian models) (e.g., Mode 1958, Seger 1988). On the other hand, quantitative trait-based models (hereafter quantitative models) assume the genetic architecture consists of many genes of small effect and produce continuous phenotypes (e.g., Saloniemi 1993, Gavrilets 1997).

Here we highlight the connection between Mendelian and quantitative models of victims and exploiters and then clarify the relationships between existing modeling frameworks for quantitative traits. We begin by reviewing the different modeling frameworks for Mendelian traits. We then draw analogies between Mendelian and quantitative models (e.g., Boots et al. 2014, Cortez and Weitz 2014). The analogies suggest that the matching framework, in which exploitation is more successful when traits "match" (i.e., a bidirectional axis of vulnerability *sensu* Abrams 2000), can arise from the difference framework, in which exploitation is more successful when traits differ (i.e., a unidirectional axis of vulnerability *sensu* Abrams 2000), in multidimensional quantitative models. Finally, as a proof of concept, we give an example model of theoretical quantitative genetics where a victim-exploiter coevolutionary dynamics arising from two pairs of difference traits can appear as a matching interaction in a single pair of traits.

BACKGROUND

Historically, in Mendelian models, two major interactions were often assumed and contrasted: the matching allele (MA) framework, in which exploitation is successful when traits match (e.g., Grosberg and Hart 2000) (Fig. 1A), and the gene-for-gene (GFG) framework, in

which a generalist exploiter can exploit a range of victim genotypes, but pays a cost for generalism (Flor 1956) (Fig. 1C). Researchers have investigated the relative importance and relationships of the two interactions (e.g., Parker 1994, Frank 1996, Agrawal and Lively 2002). Recently, Ashby and Boots (2017) found that, in multidimensional Mendelian (multilocus) models, the GFG framework can behave effectively as the MA framework (Fig. 2A).

To illustrate, consider a simple GFG model with haploid victims and exploiters with two loci with two alleles each, labelled 1 and 0. The alleles 1 and 0 indicate the presence and absence, respectively, of an exploitation or defense trait (Fig 2A). If both of the allelic values of the exploiter are greater than or equal to those of the victim, maximum exploitation will occur (black squares in Fig. 2A). If the victim has exactly one allelic value greater than that of the exploiter, so that the other allelic value of the victim is less than or equal to the corresponding value of the exploiter, then exploitation will be partial (gray squares in Fig. 2A). Finally, in the case where both allelic values of the victim are strictly greater than that of the exploiter (which only occurs when the victim has genotype 11 and the exploiter has 00), then the victim is defended against exploitation (a white square in Fig. 2A).

When coevolutionary dynamics occurs between four genotypes with the alleles 1 and 0,

76 the type of interaction (indicated by a dashed white line in Fig. 2A) effectively reduces to a MA

77 interaction: the exploiter genotype 01 (10) is more successful at exploiting its matching counter

78 victim genotype 01 (10) as in Fig 1A. Indeed, by investigating a multilocus GFG model, Ashby

79 and Boots (2017) found that, in the case where an intermediate number of alleles is optimal, the

80 victim/exploiter genotypes alternate between various subsets of defense/exploitation alleles, but

81 the total number of alleles stays constant. Hence, the multidimensional GFG framework

82 effectively behaves as the MA framework (Fig. 2A).

83 As with Mendelian models, quantitative models have assumed an apparent dichotomy

84 between two frameworks (Abrams and Matsuda 1997, Abrams 2000, Gilman et al. 2012, McPeek

85 2017): the matching trait framework, in which exploitation is increasingly more successful with

86 the extent that trait values of exploiters match those of victims (Fig. 1B), and the difference trait

87 framework, in which exploitation is increasingly more successful with the extent that trait values

88 of exploiters exceed those of victims (Fig. 1D). They are also known as the bidirectional and

89 unidirectional trait cases, respectively (Abrams 2000). The matching framework is analogous to

90 the MA model and is used, for example, when an exploiter can best exploit a victim with body

91 size or color within a certain range (Brown and Vincent 1992, Marrow et al. 1992, Dieckmann et

al. 1995, Gavrilets 1997, Khibnik and Kondrashov 1997, Nuismer et al. 2005, Kopp and Gavrilets 2006, Calcagno et al. 2010, Dercole et al. 2010, Mougi 2012, Yamamichi and Ellner 2016, Fleischer et al. 2018). This has been observed in the coevolution between the African tawny-flanked prinia and its brood parasite, the cuckoo finch: the parasite varies its egg color to match that of the victim (Spottiswoode and Stevens 2012). On the other hand, the difference framework is analogous to the GFG model and is appropriate when exploitation success is determined by speed vs. speed, strength vs. armor, or toxicity vs. resistance (Saloniemi 1993, Frank 1994, Sasaki and Godfray 1999, Nuismer et al. 2007, Mougi and Iwasa 2010, Mougi and Iwasa 2011, Tien and Ellner 2012, Northfield and Ives 2013, Cortez and Weitz 2014, Yamamichi and Miner 2015, van Velzen and Gaedke 2017). For example, garter snakes evolve stronger resistance to rough-skinned newt toxicity in areas where newts are more toxic (Brodie III and Brodie Jr 1990).

In the matching framework, exploitation success is typically a unimodal function of the trait difference, and is often modeled as a Gaussian: $\exp[-(x-y)^2]$, where x and y are traits of victims and exploiters, respectively (Fig. 1B) (e.g., Gavrilets 1997, Khibnik and Kondrashov 1997, Nuismer et al. 2005, Mougi 2012). On the other hand, in the difference framework,

exploitation success is often modeled as a sigmoidal function of the trait difference: $1/[1 + \exp(x - y)]$ (Fig. 1D) (e.g., Nuismer et al. 2007, Mougi and Iwasa 2010, van Velzen and Gaedke 2017). In this framework, it is always advantageous for both species to increase the trait values for better exploitation/defense (McPeek 2017). Empirical evidence suggests that there is an energetic trade-off to exploitation and defense and hence, most models of difference traits assume there is a cost associated with each trait, which prevents runaway evolution. For example, garter snakes resistant to newt toxin have costs associated with slower sprinting speeds (Brodie III and Brodie Jr 1999), milkweed bugs' production of enzymes to break down milkweed toxins has metabolic costs (Dalla and Dobler 2016), and numerous plants produce defense chemicals with a cost to plant growth (reviewed in Herms and Mattson 1992).

Here, by drawing analogies between the Mendelian trait and quantitative trait frameworks (Fig. 1), we further extend the generalization of Ashby and Boots (2017) and demonstrate that the difference framework can result in similar dynamics to the matching framework in multidimensional quantitative models. The matching model is a continuous trait analog to the MA model and the difference model is a continuous trait analog to the GFG model (Fig. 1). In a multilocus GFG model, under certain conditions the victim/exploiter genotypes

alternate between various subsets of defense/exploitation alleles, but the total number of alleles stays constant, which is effectively what occurs under the MA framework (Ashby & Boots 2017). This is analogous to a bivariate difference trait model, in which the victim/exploiter genotypes alternate between having more investment in one defense/exploitation trait vs. another, which is effectively what occurs under the matching framework. Instead of switching between the extremes of a single matching trait, the species are switching between two difference-trait-based strategies. Here, we consider a victim-exploiter model in which each has two difference traits that influence exploitation success. An empirical example that motivates our study is a stepwise infection process (Hall et al. 2017), where host species prevent exploitation of parasites by several difference traits. In the case where intermediate trait values are optimal due to the costs of defense/offense, the victim/exploiter traits may switch between combinations where a trait is large while the other trait is small, but the total costs stay constant. The resultant dynamics may appear as the matching interaction, and this is the quantitative-model analog to the findings in Ashby and Boots (2017) in Mendelian models.

AN EXAMPLE

We develop a two-dimensional quantitative model with difference interactions (Fig. 2B) to demonstrate that matching dynamics can emerge from a multidimensional difference framework (see Appendix and Supplementary Mathematica file for details). We consider a quantitative genetic model (Lande 1976, Iwasa et al. 1991) in continuous time (i.e., Malthusian fitness) (Abrams et al. 1993). We assume that victims and exploiters each have two quantitative traits. We let x_i be the value of victim trait i (= 1, 2) and assume greater values allow for defense against trait i of the exploiter. We let y_i be the value of exploiter trait i and assume greater values allow for more exploitation. Each trait is associated with a cost that decreases individual fitness with greater trait values. The difference between the exploiter trait and the corresponding victim trait, $y_i - x_i$, affects exploitation success (Fig. 2B), which is expressed by a sigmoid function (Fig. 1D). We assume that fitness of victims and exploiters are, respectively,

$$\begin{aligned} W_x &= r\left(x_1, x_2\right) - a_0 \prod_{i=1}^{2} \frac{1}{1+\exp\left[-\theta_i\left(y_i - x_i\right)\right]}, \\ W_y &= c\left(y_1, y_2\right) a_0 \prod_{i=1}^{2} \frac{1}{1+\exp\left[-\theta_i\left(y_i - x_i\right)\right]}, \end{aligned} \tag{1}$$

where a_0 is the effects of successful exploitation on fitness (e.g., maximum attacking rate), and θ_i (i = 1, 2) determine the sensitivity of exploitation success to the trait difference. We assume that victims need to overcome their exploiters at only one trait for escaping from exploitation, whereas exploiters must overcome the two defense traits for successful exploitation (Gilman et al. 2012). This sequential interaction is also found in many host-parasite systems (Hall et al. 2017).

Here r and c represent costs of defense and exploitation for victims and exploiters, respectively (e.g., prey growth and predator conversion efficiency are decreasing functions of defense and offense, respectively: see Appendix S1), and they are linearly decreasing functions of the sum of the two traits values (i.e., lower values of r and c represent higher costs). In addition, we add stabilizing selection to the victim cost function as in Gavrilets (1997) to prevent runaway evolution to infinite trait values. This can occur in quantitative models but not in Mendelian models because it is customary to assume unbounded trait values in quantitative models, which permits the existence of runaway escalation, whereas Mendelian traits are typically modeled as taking values in finite sets. We employ the following functions:

$$r = r_0\left(1-\sum_{i=1}^{2}\rho_{xi}x_i\right)\exp\left[-\sum_{i=1}^{2}s_i\left(x_i-x_{i0}\right)^2\right],$$
$$c = c_0\left(1-\sum_{i=1}^{2}\rho_{yi}y_i\right), \tag{2}$$

where r_0 and c_0 are basic parameter values (e.g., for prey growth rate and predator conversion efficiency) and ρ_{ij} ($i = x, y, j = 1, 2$) determine the slope of the functions. Stabilizing selection drives victim evolution toward $(x_1, x_2) = (x_{10}, x_{20})$, where s_i ($i = 1, 2$) determines the strength of stabilizing selection.

Then coevolutionary dynamics are described by four ordinary differential equations,

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} v_{x11} & v_{x12} \\ v_{x12} & v_{x22} \end{pmatrix}\begin{pmatrix} \dfrac{\partial W_x}{\partial x_1} \\ \dfrac{\partial W_x}{\partial x_2} \end{pmatrix},$$
$$\frac{d}{dt}\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} v_{y11} & v_{y12} \\ v_{y12} & v_{y22} \end{pmatrix}\begin{pmatrix} \dfrac{\partial W_y}{\partial y_1} \\ \dfrac{\partial W_y}{\partial y_2} \end{pmatrix}, \tag{3}$$

where v_{ijj} ($i = x, y, j = 1, 2$) represents additive genetic variance, v_{i12} ($i = x, y$) represents

180 covariance, and partial derivatives represent fitness gradients (Abrams et al. 1993). For simplicity,

181 we assume that the traits evolve independently (genetic covariance, v_{j12}, is zero). This is likely in,

182 for example, hosts that defend against parasites by a cellular immune response and a behavioral

183 response, but further work is needed to explore the effects of trait correlations. We also assume

184 trait symmetry, but this should be carefully examined in future studies as the symmetry will be

185 broken with probability one in the real world (Fig. S4).

186 By numerically solving the model, we find that the two-dimensional difference model

187 can behave as a one-dimensional matching model. First, when there is no stabilizing selection in

188 the victim cost ($s_i = 0$) and the exploiter genetic variance is small enough ($v_{xii} >> v_{yii}$, $i = 1, 2$),

189 coevolutionary dynamics shows runaway escalation toward extreme trait values, and the

190 coevolutionary outcome depends on initial conditions (Fig. S2). Second, when there is stabilizing

191 selection ($s_i > 0$) and the exploiter genetic variance is large enough (e.g., $v_{xii} < v_{yii}$), the system is

192 attracted to a stable equilibrium (the blue and red points in Figs. 3A, 3B), and there is disruptive

193 selection for victim traits (i.e., fitness minimum: vectors representing fitness gradients in Figs. 3A

194 are distracted from the equilibrium) and stabilizing selection for exploiter traits (i.e., fitness

195 maximum: vectors in Figs. 3B are attracted to the equilibrium), which is consistent with the

matching interaction (Appendix S2) (Abrams and Matsuda 1997, Gavrilets 1997). Third, when there is stabilizing selection ($s_i > 0$) and the exploiter genetic variance is small enough ($v_{xii} >> v_{yii}$), the equilibrium is not stable (Appendix S3, Fig. S3) and the trait dynamics fluctuate (Fig. 3C) but are constrained to regions in which the total investments are nearly constant (Fig. 3D) and the two traits for each species show antiphase cycles (Figs. 3C, E, F). These simulation results demonstrates that the matching dynamics can arise from the difference interaction, generalizing Ashby and Boots (2017)'s idea from Mendelian models to quantitative models.

DISCUSSION

Victim-exploiter interactions are among the most fundamental type of ecological interactions. In addition to their importance in ecological communities, these interactions are widely recognized for playing an important role in ecological dynamics (e.g., extinction and predator-prey cycles: Northfield and Ives (2013), Cortez and Weitz (2014)) and evolutionary dynamics (e.g., sex, recombination, and epistasis: Otto and Lenormand (2002)), because each species needs to continue to adapt to new selection pressures by the other species. Due to its importance, many modeling frameworks have been proposed to investigate the dynamics of

212 coevolution between a victim and its exploiter, capturing various aspects of the traits

213 involved (Nuismer 2017).

214 In this work, we highlight the relationship between two modeling frameworks of

215 quantitative traits in victim-exploiter coevolution. In particular, a multidimensional difference

216 trait framework, in which each trait confers an advantage in the victim-exploiter interaction but is

217 associated with some cost (Figs. 1D, 2B) can generate dynamics like a matching trait framework,

218 in which traits between a victim and exploiter must "match" in some sense for successful

219 interactions (Fig. 1B). Our investigation extends our knowledge of the coevolutionary process by

220 demonstrating how effectively matching dynamics can be generated from difference traits in a

221 special case of multivariate coevolution as a proof of concept (rather than a thorough

222 investigation of the dynamics: Fig. 3).

223 For some traits, the distinction between matching traits and difference traits is clear. For

224 both victims and exploiters, being stronger and faster are always more advantageous (but may

225 have an associated cost or energetic limitation) and hence, are difference traits. However, in other

226 cases, it is not so obvious. For example, body size of both victims and exploiters can be a

227 difference trait, in which bigger is better for exploitation/defense (e.g., gape-limited predation), or

228 a matching trait, in which exploiters must be within a certain size range depending on victims'

229 size for successful exploitation. Our simulations suggest that, even when the body size is a

230 difference trait, it may behave as a matching trait because of another difference trait. This

231 correlated coevolution between the two traits can occur even without genetic covariance, as long

232 as the costs of being big affect fitness together with the cost of the other trait.

233 Previous work has suggested that matching traits are more likely to lead to

234 coevolutionary cycling of traits than difference interactions (Abrams 2000, McPeek 2017). In

235 comparing quantitative models with a one-dimensional trait, for example, McPeek (2017) found

236 cycles are observed in a smaller area of parameter space with difference traits compared to

237 matching traits. Furthermore, the underlying mechanism of cycles differs in the two frameworks.

238 In the matching framework, cycles consist of the exploiter tracking victim traits and the victim

239 escaping from exploiter traits (i.e., fluctuating selection between equally specific

240 defense/exploitation traits). In the difference framework, cycles consist of the victim and

241 exploiter investing more energy in their traits for better defense/exploitation, and then

242 abandoning their defense/exploitation because at some point they are too costly to maintain (i.e.,

243 fluctuating selection between strong and weak defense/exploitation traits). Even when empirical

244 researchers are focusing on a single trait with the difference interaction, the system may have
245 another difference trait that can affect exploitation success. In such a case, coevolutionary
246 dynamics can be driven by the matching-like interaction, which may cause cyclic dynamics more
247 easily (McPeek 2017).

248 In spite of recent interest in coevolution in multidimensional trait space (e.g., Gilman et
249 al. 2012, Débarre et al. 2014, Doebeli and Ispolatov 2017), the relation of the matching and
250 difference frameworks has not been well recognized. For example, in their study on evolutionary
251 escape, Gilman et al. (2012) contrasted coevolutionary dynamics with matching and difference
252 interactions in multidimensional trait space but did not find a significant difference between them
253 (see Fig. 1 of Gilman et al. (2012)). Our generalization offers a potential explanation for this
254 previous work, as coevolutionary dynamics with matching interactions can arise from difference
255 interactions in multidimensional quantitative models.

256 This work was inspired by the recent work of Ashby and Boots (2017), who showed an
257 analogous relationship for two Mendelian trait models of coevolution. Here, we draw out the
258 parallels between two Mendelian (single-locus) trait frameworks and two quantitative trait
259 frameworks. Namely, we highlight that the matching allele (MA) framework is a Mendelian

analog of the matching framework, and the gene-for-gene (GFG) framework is a Mendelian analog of the difference framework (Fig. 1). While these frameworks are valuable, many traits important to victim-exploiter interactions may actually lie somewhere in the middle of these two extremes; they may be determined by many (but not infinite number of) loci. It is still not well understood how coevolutionary dynamics differ between when traits are governed by a single locus, multi-locus (with linkage disequilibrium and epistasis), and effectively infinite loci (as assumed in classical quantitative genetics). While there have been a handful of papers to investigate this question in specific scenarios, further investigation is need for a general understanding.

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FIGURE LEGENDS

Figure 1. Interaction frameworks and genetic architectures in coevolution models. A: Matching allele (MA) is a matching interaction in Mendelian traits. Here victims and exploiters are haploid and their genotypes are represented by 1 and 0 at a particular locus, and they indicate the presence and absence, respectively, of defense/exploitation alleles. Dark shading indicates greater exploitation success. B: The matching interaction is a MA interaction in quantitative traits. Exploitation success is maximized when the trait difference is zero. C: Gene-for-gene (GFG) is a difference interaction in Mendelian traits. D: The difference interaction is a GFG interaction in quantitative traits. Exploitation success is increased by larger exploiter trait values and by smaller victim trait values.

Figure 2. A: An example of exploitation matrix in a Mendelian GFG model with two loci (Ashby and Boots 2017). The region surrounded by a dashed white line shows that the MA interaction arises from the GFG framework. Victims and exploiters are haploid and their genotypes are represented by 1 and 0 at a locus, and they indicate the presence and absence, respectively, of defense/exploitation alleles. Darker shading indicates greater exploitation success and arrows

401 indicate greater costs. B: Exploitation success as a function of both trait differences between

402 exploiters and victims ($y_i - x_i$) in a quantitative difference model with two traits (Eq. 1).

403

404 **Figure 3.** Coevolutionary dynamics of two quantitative traits with difference interactions. A, B:

405 Fitness landscapes of victims (A) and exploiters (B) when the exploiter genetic variance is large

406 enough and the system converges to a stable equilibrium. A: A contour plot of fitness (W_x) and a

407 vector field of fitness gradients for the victim traits when the exploiter traits are at the equilibrium

408 trait value (the red point in B). B: A contour plot of fitness (W_y) and a vector field of fitness

409 gradients for the exploiter traits (B) when the victim traits are at the equilibrium trait value (the

410 blue point in A). Parameter values are $\rho_{xi} = 0.07$, $\rho_{yi} = 2$, $x_{10} = x_{20} = 0.2$, $a_0 = r_0 = c_0 = \theta_i = v_{jii} = 1$,

411 $s_i = 0.01$, and $v_{j12} = 0$ ($i = 1, 2, j = x, y$). C-F: Coevolutionary cycles when the victim genetic

412 variance is much larger than exploiter genetic variance ($v_{xii} >> v_{yii}$). C: Numerical solutions of the

413 four traits. D: Numerical solutions of the functions (Eq. 2) representing costs of

414 defense/exploitation (note that lower values indicate higher costs). E, F: Coevolutionary cycles of

415 victims (E) and exploiters (F). Parameter values are the same as A and B except for $v_{xii} = 1$ and

416 $v_{yii} = 0.01$ ($i = 1, 2$). Note that c is negative in gray regions in B and F.

Figure 1.

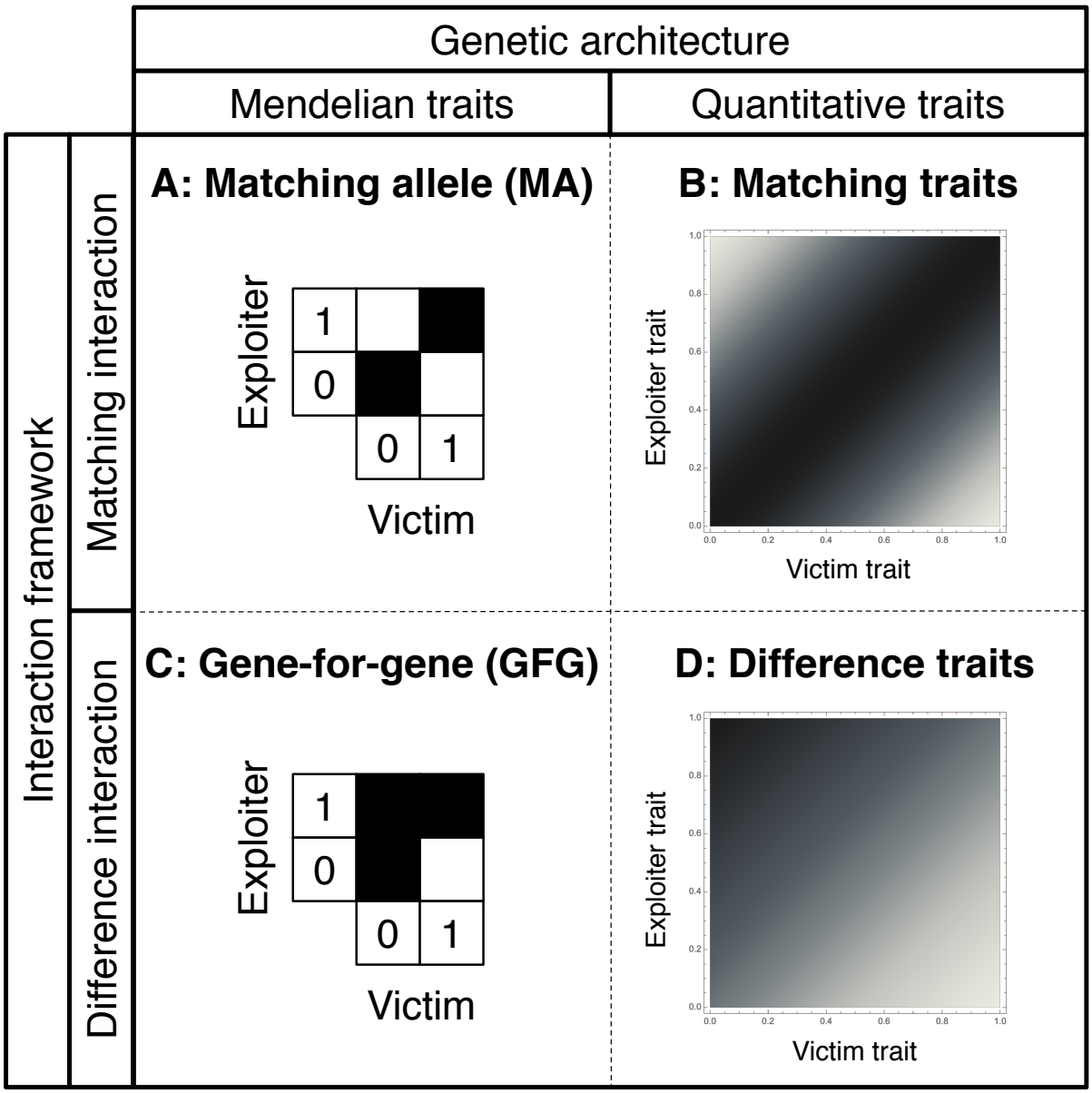

Genetic architecture
Mendelian traits
Quantitative traits
Interaction framework
Matching interaction
Difference interaction
A: Matching allele (MA)
Exploiter
1
0
0
1
Victim
B: Matching traits
Exploiter trait
Victim trait
C: Gene-for-gene (GFG)
Exploiter
1
0
0
1
Victim
D: Difference traits
Exploiter trait
Victim trait

Figure 2.

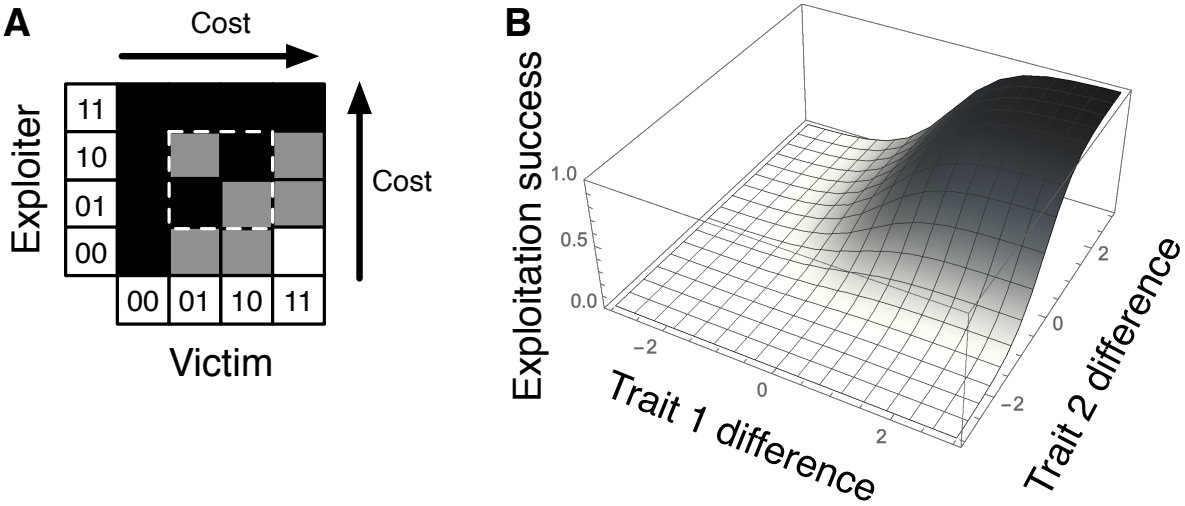
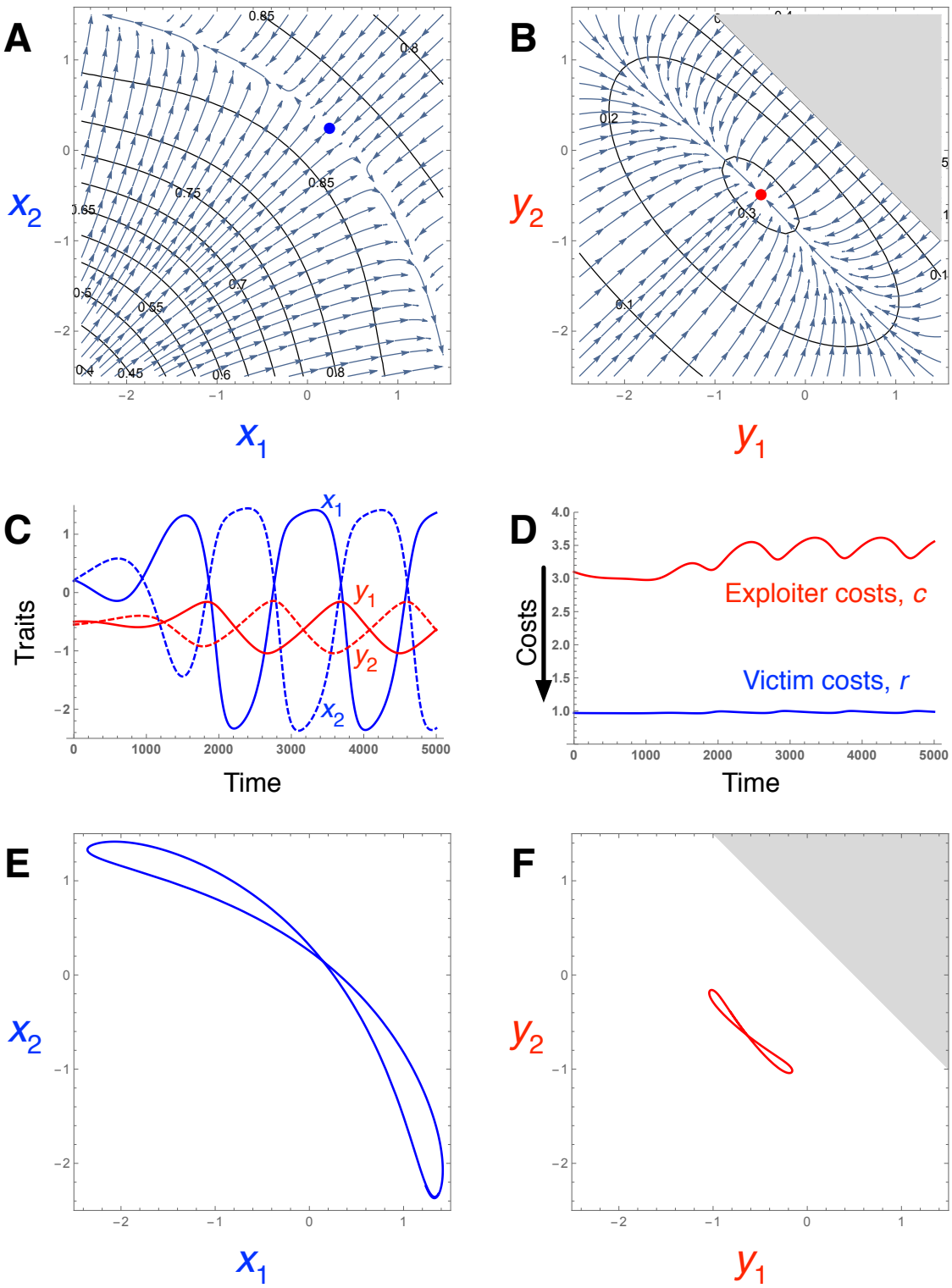

A
Cost
Cost
Exploiter
11
10
01
00
00
01
10
11
Victim
B
Exploitation success
1.0
0.5
0.0
−2
0
2
Trait 1 difference
2
0
−2
Trait 2 difference

Figure 3.


A
B
C
D
E
F
x_1
x_2
y_1
y_2
Traits
Time
Costs
Exploiter costs, c
Victim costs, r